# The ocean has depth: two- versus three-dimensional space use estimators in a demersal reef fish

**K. A. Lee[1],\*, C. Huveneers[2,3], T. Duong[4], R. G. Harcourt[1]**

[1]Department of Biological Sciences, Macquarie University, North Ryde, Sydney, Australia
[2]Threatened, Endangered, and Protected Species subprogram, SARDI – Aquatic Sciences, Adelaide, Australia
[3]School of Biological Sciences, Flinders University, Adelaide, Australia
[4]Theoretical and Applied Statistics Laboratory, University Pierre and Marie Curie-Paris 6, Paris, France

ABSTRACT: Most aquatic animals employ 3-dimensional (3D) movements to fully exploit the resources of the environment they inhabit. Many of these animals, however, are impossible to observe directly, making it necessary to use indirect methods of observation such as biotelemetry in order to study them. Despite technological advances with tracking equipment enabling movement to be assessed in 3 dimensions, many studies restrict their analyses to traditional 2-dimensional (2D) space use. We compared 2D and 3D (1) core and home range size, (2) home range overlap and (3) changes in space use in relation to biological and environmental variables of a large, demersal reef-dwelling fish species, the eastern blue groper *Achoerodus viridis*, tracked using passive acoustic telemetry. Mixed effects models were used to determine differences between the core/home range sizes and home range overlap between the sex of the fish and the breeding and non-breeding seasons. The 2D analyses were unable to detect differences in core and home range sizes between the sexes that were successfully identified by the 3D analyses. 2D analyses only detected differences in home range overlap between the breeding and non-breeding seasons, whereas the 3D analyses found seasonal differences according to the sex of the fish. Two-hourly 2D space use estimates failed to detect differences in space use between fished and protected areas that were detected in the 3D analyses. This study demonstrates that to truly understand how animals use the space they inhabit, we must assess their movement in the full spatial context of their environment.

KEY WORDS:  Utilization distribution · Passive acoustic telemetry · Home range · Territoriality · Labridae · *Achoerodus viridis* · Eastern blue groper · IMOS-AT

## INTRODUCTION

Advances in telemetry have provided biologists with a wealth of sophisticated techniques to study the behaviour, physiology and ecology of animals at varying spatio-temporal scales (see review by Hussey et al. 2015). These techniques have been implemented across a wide variety of taxa, from small insects to large aquatic animals, and have proven invaluable for species where opportunities for obser-

vational studies are limited (Cooke et al. 2004). How long animals spend in specific areas, whether they use well-defined home ranges or whether their space use changes over time are a few of the critical ecological research questions (see review by Pittman & McAlpine 2003) that telemetry is being used to address. For example, in conservation-based ecology, the understanding of fish movement has been used to determine the appropriate size, placement and connectivity between marine protected areas

(Pittman et al. 2014, Green et al. 2015, Weeks et al. 2017), or to quantify key abiotic factors affecting movement (e.g. Avgar et al. 2013, Bestley et al. 2013, 2015, Dudgeon et al. 2013). In behavioural ecology, telemetry has been used to assess foraging ecology (e.g. Shiel et al. 1999, Harcourt et al. 2002, Heide-Jørgensen et al. 2012), interactions between conspecifics (e.g. Stehfest et al. 2013, Wey et al. 2013), territoriality (e.g. Lebsock et al. 2012, Pérez-García et al. 2013) or combinations of all 3 (Harcourt et al. 2007).

Animal movements result from a complex interplay between biotic factors (food, predator avoidance, mates) and abiotic factors (thermal regimes, salinity gradients, physical shelter) (Hays et al. 2016). To understand how animals will respond to changes in their environment (e.g. changes due to climate change) or through removal of conspecifics (e.g. fishing), we must first identify the biotic and abiotic factors that are driving these space use patterns. However, in order to adequately do this, the spatial scale in which an animal uses its environment must be incorporated into analyses (Pittman & McAlpine 2003, Börger et al. 2006, Bestley et al. 2015). All aquatic species live in a 3-dimensional (3D) environment and exploit their surroundings by employing 3D movements. However, despite the technology being available to measure 3D movement, the majority of studies in the marine environment to date have restricted analyses to 2-dimensional (2D) movements and analysed the third dimension (e.g. depth) separately (e.g. Bryars et al. 2012, Currey et al. 2014, Lee et al. 2015). While 2D analyses remain important for incorporation in marine spatial planning, to compare between studies and to address habitat-use questions, studies that have used 3D analyses have resulted in an increased depth of understanding that would not be possible with 2D analyses. For example, 3D dive profiles of Weddell seals revealed foraging and co-specific behaviour that would not have been possible with 2D analyses (Davis et al. 1999, Harcourt et al. 2000, Hindell et al. 2002).

The range of estimators available to quantify space use has rapidly increased over recent years (see Powell 2000, Kie et al. 2010, Fieberg & Borger 2012). Although the choice of the most appropriate estimator will be study-specific, Signer et al. (2015, p. 8) showed that the relative differences between estimators are negligible and they concluded that there should be more 'emphasis on whether the [space use] estimator does a good job of capturing an important biological signal in the data'. This, combined with ensuring that the data are analysed within the same spatial scale as the animal's movement, has led to an increasing use of multidimensional data to explore space use patterns (e.g. Keating & Cherry 2009, Cooper et al. 2014, Tracey et al. 2014). Kernel utilization densities (KUDs), a popular choice of estimators which are robust against serially auto-correlated data (de Solla et al. 1999, Fieberg 2007) and are generally easy to use (Kie et al. 2010), have recently been extended to analyse multidimensional data (Duong 2007). For example, Simpfendorfer et al. (2012) found that 2D KUDs overestimated overlapping home ranges by up to 20% compared to 3D KUDs due to individuals using different water depths within the same latitudinal and longitudinal location (see also Cooper et al. 2014). Such overestimation may mask possible social behaviours (such as territoriality) or reduce the ability to detect niche partitioning between competitors if the animals being studied employ 3D movements. In addition, 3D KUDs have been used to detect diel changes in space use and habitat use of sea snakes (*Hydrophis* [*Lapemis*] *curtus* and *H. elegans*) in relation to predator–prey relationships (Udyawer et al. 2015b), and to identify the environmental variables driving movement of one of these species (*H. curtus*; Udyawer et al. 2015a). However, these studies used a pairwise comparison of the proportion of total home range size that each animal overlapped with, which has been suggested to overestimate the degree of overlap between individuals as it ignores the relative probability of use (i.e. utilization distribution; Fieberg & Kochanny 2005). Overlap indices that are a function of utilization distribution have been recommended to take this into account (Fieberg & Kochanny 2005).

Furthermore, to our knowledge, all marine-based studies to date that have used 3D space use analyses have done so on pelagic species that occupy the entire water column. This is despite studies on terrestrial animals having shown that incorporating topographical data into the analyses can provide better estimates for home range sizes (Greenberg & McClintock 2008, Monterroso et al. 2013), suggesting that 3D space use analyses are also likely to be relevant for demersal or substrate-associated species. This implies that there is a need to determine whether 3D modelling of KUDs is able to detect the influence of biological or environmental variables on space use better than 2D models for demersal fish that inhabit topographically heterogeneous reef environments.

Eastern blue gropers *Achoerodus viridis* (Labridae) are the largest benthic reef fish found in temperate south-eastern Australia (Gillanders 1999).

They can grow up to 120 cm total length (Kuiter 1996) and live up to 35+ yr (Gillanders 1995a). They occur from southern Queensland to central Victoria (Gomon et al. 2008), with the highest densities found in New South Wales (NSW). Adults inhabit coastal and estuarine rocky reefs, up to a depth of 60 m (Gomon et al. 2008), and are found in similar abundance along different reef habitat types (Gillanders & Kingford 1998, Curley et al. 2003). They have high levels of site fidelity and occupy small home ranges (Lee et al. 2015). Like many labrids, they are monandric protogynous hermaphrodites. They mature as females at approximately 1–2 yr (22–28 cm standard length, SL) and transform into males at 10+ yr (50–58 cm SL), although females have been recorded up to 18+ yr (Gillanders 1995a). The population sex ratio is biased towards females (Gillanders 1995a), and although no studies have been conducted on the social structure of the eastern blue groper, males are thought to dominate over a harem of females since territoriality and dominance hierarchies are frequently observed in protogynous fish species (Warner & Swearer 1991, Mumby & Wabnitz 2002, Raposeiro & Azevedo 2009, Kline et al. 2011). Within such social structures, terminal-phase males will usually aggressively defend a territory against intruders and large females (see Kline et al. 2011 and references therein). Such aggressive behaviour has been linked to an increase in fishing mortality in other protogynous hermaphrodite species (Gilmore & Jones 1992), and removal of large males may lead to lower fertilisation rates due to a reduction in spawning males (Gillanders 1995a). Therefore, accurate knowledge of social structures are vital for the management of this long-lived species. One method that can measure territoriality is to calculate the amount of home range overlap between individuals (e.g. Nemtzov 1997). However, it is important to use the appropriate indices that are a function of the individuals' utilization distributions.

The present study tracked eastern blue gropers using passive acoustic telemetry to demonstrate the importance of analysing movement parameters within the spatial context of their environment. The specific objectives were to test whether: (1) separate 2D analyses of horizontal (core and home range) and vertical (depth) movements detected the same inter-seasonal (breeding/non-breeding seasons) differences between sexes as 3D analyses; (2) 2D analyses detected the same levels of home range overlap between different sex pairings as 3D analyses; and (3) the environmental and biological parameters influencing short-term space use was the same for 2D and 3D analyses.

## MATERIALS AND METHODS

### Study site

This study was conducted in the Bronte-Coogee aquatic reserve, a small marine protected area 10 km south of Sydney Harbour, NSW, Australia (33° 54′ S, 151° 16′ E). The reserve encompasses a total area of 0.43 km$^2$, with a central 0.16 km$^2$ no-take section for eastern blue gropers *Achoerodus viridis* (Fig. 1). The remainder of the reserve permits line fishing of eastern blue gropers (hereby referred to as the 'unprotected' area). It comprises areas of high- and low-relief rocky reef, consisting of typical habitats found along the NSW coast (e.g. urchin-grazed barrens, *Ecklonia* forest; Underwood et al. 1991). These slope onto a sandy bottom at 10–25 m depth. A habitat map of the study site and surrounding areas was pro-
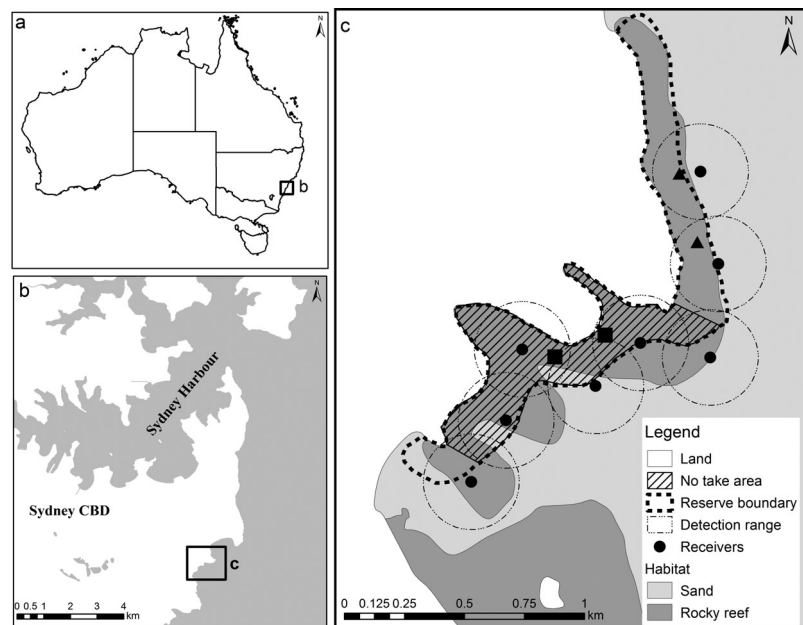


Fig. 1. Habitat map of Bronte-Coogee Aquatic Reserve (BCAR) showing (a) the location of the study site in relation to Australia and (b) to Sydney Harbour. (c) A close-up of BCAR showing the acoustic telemetry array. Black squares indicate where fish were tagged in the no-take area and black triangles indicate where fish were tagged in the 'unprotected' area

duced from multi-beam sonar by the Office of Environment and Heritage NSW following methods detailed by Jordan et al. (2010), providing the reef structure and depth contours of the whole area.

## Acoustic tracking

Eight stationary underwater receivers (VR2W, Vemco) were placed both inside and along the boundary of the reserve (Fig. 1) from 3 July 2009 and 23 June 2010 using bottom moorings 1.5 m above the seabed. Range testing was conducted to determine the effective detection range of the receivers using methods described by Heupel et al. (2006), and was estimated at a minimum of 300 m radius for the worst oceanic conditions, which led to receivers having an overlapping detection range in most of the reserve. A sentinel tag, the same model as the animal tags (see next section), was deployed in a stationary position within range of a single receiver (R4) to determine variation in acoustic detectability. The tag was deployed for a total of 40 d during variable environmental conditions.

Eastern blue gropers were caught using barbless baited circle hooks on monofilament line from depths <20 m. Although sampling was conducted throughout the reserve, fish were only caught in 4 locations (see Fig. 1); 2 within the no-take area and 2 within the 'unprotected' area of the reserve. Once aboard the research vessel, an acoustic transmitter equipped with a pressure sensor (accuracy ± 1.7 m when deployed at a maximum depth of 34 m, see https://vemco.com/wp-content/uploads/2014/05/v13-coded.pdf; V13-1P with a pulse interval of 120–240 s) was surgically implanted into the peritoneal cavity using surgical techniques described by Lee et al. (2015). During recovery, the total length of each fish was measured to the nearest centimetre, and the sex of the fish was designated following Gillanders (1995a), who found that all individuals <50 cm SL were female, while individuals >58 cm were male. All fish between 50 and 58 cm were classified as 'indeterminate sex'. Data from the first 36 h post-tagging were excluded due to potential atypical behaviour as a result of the tagging. Lee et al. (2015) showed that eastern blue gropers exhibit long residency times within the study area, with 67% of the fish detected within the reserve for 90% of the study time (345 d). The number of receivers that detected eastern blue gropers varied throughout the day from fish being detected by only 1 receiver at night but up to 7 receivers at noon.

## Data analysis

### Estimation of *x* and *y* coordinates

The *x* and *y* coordinates of the fish detections were calculated using methods described by Lee et al. (2015), whereby the 300 m detection range for each receiver was overlaid with depth contours using ArcGIS 9.3 (ERSI). This produced polygons containing the area in which fish may be located for each receiver/depth combination. To account for the depth sensor precision of ±1.7 m, the polygons were extended vertically to include depths within ±1.7 m of the recorded fish depth and rounded to the nearest 2 m (to match the bathymetry contours which were measured at 2 m increments), resulting in a 3D area where fish were most likely to be when detected (Fig. 2a). This 3D area was then extended horizontally (offshore) until the distance between the substrate and the lower (deeper) limit of the 3D area was 4 m, to account for situations when eastern blue gropers were slightly above the reef (Fig. 2b). The 4 m threshold was selected because eastern blue gropers are reef-associated benthic carnivores with high rates of feeding (8.97 ± 1.27 bites per 5 min period; Gillanders 1995b), and *in situ* observations showed few excursions by eastern blue gropers away from the substrate (K. A. Lee, R. G. Harcourt & C. Huveneers pers. obs.). The *x* and *y* coordinates were then estimated by randomly selecting a point anywhere inside the obtained 3D area for each of the detections.

### Home range size estimates and depth utilisation

The home range of an animal is commonly estimated using KUD, with 50 and 95% contours representing the core and home range size, respectively (e.g. Parsons et al. 2010, Simpfendorfer et al. 2012). We calculated the 2D (area) and 3D (volume) KUDs for the breeding and non-breeding season using the 'kde' function in the 'ks' package (Duong 2007) in R. A plug-in bandwidth selector was used to estimate the smoothing factor using the 'Hpi' function in the 'ks' package. This bandwidth selector was used, as it has been shown to perform well with most data distributions in home range studies (Gitzen et al. 2006) and to produce the same KUDs as the smoothed cross-validation (Chacón & Duong 2011). The same *x* and *y* coordinates were used for each 2D and corresponding 3D core and home range estimate, with the 3D estimate using the depth value recorded as the additional dimension. The breeding season was de-
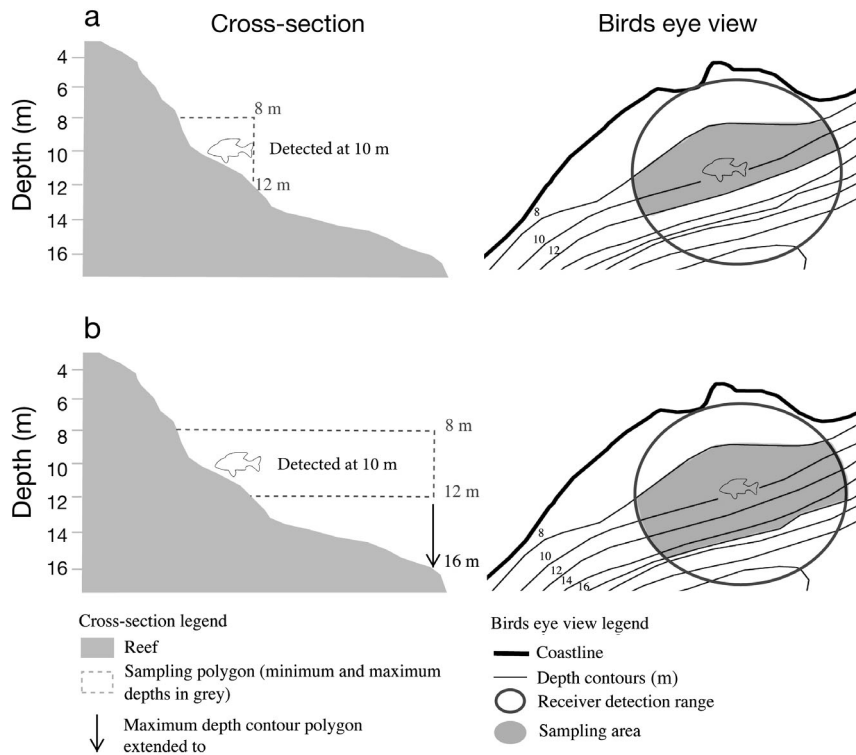
Fig. 2. A diagram showing how the polygons in which the *x* and *y* coordinates were randomly sampled accounting for (a) tag error (±1.7 m, rounded to ±2.0 m), and (b) tag error and fish being within 4 m of the reef

fined as July to the end of October (Gillanders 1995a) and the non-breeding season as January to the end of April (i.e. excluding November, December, May, and June to ensure no overlap of seasons).

Linear mixed models (LMMs) were used to determine if there were any differences in core and home range sizes between seasons and sexes for 2D and 3D KUD estimates. Since a potential difference in core or home range size between seasons according to sex was of interest, an interaction between season and sex was tested. The unique fish identity code was used as the random effect to allow for repeated measures from the same individuals. KUDs were non-normally distributed and had to be log- or square-root transformed to meet the assumptions of normality and homogeneity of variance. Data exploration was conducted following the general protocol of Zuur et al. (2010) that used Cleveland dot plots, boxplots, and scatterplots to identify patterns and outliers in the observations. The 'best' model structure was found following a step-down protocol, set out in Zuur et al. (2009). The R (R Core Development Team 2009) 'nlme' package (Pinheiro et al. 2013) was used for the LMMs. Support for each model was measured using the differences in Akaike's information criterion

corrected for small sample sizes (ΔAICc) where the 'best' model ΔAICc is 0 and ΔAICc values below 10 show models with reasonable support (Burnham & Anderson 2002). If ΔAICc showed support for more than 1 model, model averaging across normalized Akaike's weights was conducted using the 'MuMIn' package in R (Barton 2012). Tukey's pairwise comparisons were used if a multi-level covariate (i.e. a categorical value with more than 2 levels, such as the sex main effect or the season and sex interaction term) was included in the 'best' model or model-averaging and were conducted using the 'multcomp' package (Hothorn et al. 2010). Otherwise, significance of a non multi-level model covariate (e.g. sex) was estimated from the 95% confidence intervals that were calculated using the 'AICcmodavg' R package (Mazerolle 2016), whereby the covariate is significant if the lower and upper confidence intervals do not cross 0 (Field et al. 2012). The relative importance of each of the fixed effects was calculated as the sum of the Akaike weights over all models in which the variable of interest appears. In order to calculate the relative importance in this way, it is important to have an equal number of models that contain each predictor variable (Burnham & Anderson 2002). Therefore, all possible combinations of the predictor variables were used to ensure that each variable was in an equal number of models. One thousand iterations of the *x* and *y* coordinate estimations, models and model selection were run to calculate the variability in the model estimates caused by the uncertainty in the fish location and tag error (see the Supplement at www.int-res.com/articles/suppl/m572p223 _supp.pdf for calculation of the optimum number of iterations).

An LMM was also used to assess whether depths (response variable) differed between the sexes and between the breeding/non-breeding seasons (explanatory variables). The unique fish identity code was used as a random intercept. The depth value used as the response variable was randomly selected to be within ±1.7 m of the recorded depth value to account for the depth sensor precision of ±1.7 m. Like the core and home-range estimations, 1000 iter-

ations of the models were run to calculate the variability in the model estimates caused by the uncertainty in the fish location and tag error. Data exploration and model selection were done using the same methods as described above.

## Home range overlap

To determine if there was a difference in the level of territoriality between the sexes and breeding/non-breeding seasons, 2D and 3D home range overlap was calculated. This was done between all fish tagged within the no-take area of the reserve using a pairwise approach, i.e. each fish compared to other fish present in that season. Only fish tagged within the no-take area were assessed as there were more individuals tagged within this section of the reserve. Inclusion of fish that were tagged within the 'unprotected' area may have produced no overlap that was only a function of the number of fish tagged within that area. Home range overlap was quantified using the utilization distribution overlap index (UDOI) that estimates the joint distribution of 2 animals' utilization distributions under the assumption that their space use is independent of each other (Fieberg & Kochanny 2005). The UDOI equals 0 for 2 home ranges that do not overlap and equals 1 for home ranges that are uniformly distributed and have 100% overlap. UDOIs >1 indicate non-uniformly distributed home ranges with a high degree of overlap (Fieberg & Kochanny 2005). The UDOI uses the area of each utilization distribution, or conditional estimates if 95% KUDs are used, estimated for each animal at a set of grid cells, which is assumed to be the same for all utilization distributions being compared (Fieberg & Kochanny 2005). To estimate the UDOIs, R codes provided by Fieberg & Kochanny (2005) were adapted for use in the 'ks' R package to estimate the KUDs across a set grid. The area (for 2D analyses) or volume (for 3D analyses) of the KUDs within each grid cell was calculated using methods described by Simpfendorfer et al. (2012).

Linear mixed-effects modelling was used to determine whether the 2D and 3D analyses could detect the same change in home range overlap between sexes and seasons. The UDOIs were used as the dependent variable with season and 'sex pairing' (the sexes of the 2 fish for which the UDOI was calculated) as the fixed effects and the identity codes of the paired fish as the random effect. Data exploration and model selection were conducted as described in the section above. A square-root transformation was used on the UDOIs to meet the assumptions of normality and homogeneity of variance.

## Space use predictors

We determined if there was a relationship between space use of fish within each 2 h time period and various environmental and biological predictors (breeding/non-breeding season, sex, location of tagging [no-take or 'unprotected' area], hour of the day [the midpoint value of a 2 h period], percentage of moon illumination, day length [h], sea surface temperature [SST] and wave height). We calculated 2D and 3D 95% KUDs for every 2 h of each day for each fish. Two-hourly KUDs were used, as fish can exhibit plasticity in diel activity (Fox & Bellwood 2011) or changes due to environmental factors (Payne et al. 2013). The same analysis was conducted on the detections from the stationary tag deployed, and the maximum 95% KUDs were considered to be representative of measurement error. Any results below the error threshold estimated from the stationary tag were deleted from the dataset. Moon illumination data were obtained from the United States Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil/data/docs/MoonPhase.php), and day length was calculated from sunrise/sunset times from the Australian Government Geoscience Australia (www.ga.gov.au/geodesy/astro/sunrise.jsp). SST and wave height were obtained through the Integrated Marine Observing System portal (IMOS 2012). The wave height data were recorded every hour, SST data were recorded every 12 min, and mean wave height and mean SST were calculated for each 2 h period.

We used generalised additive mixed modelling (GAMM) with the identity link function to determine the relationship between 2-hourly space use, various environmental and biological predictors, and an interaction between the breeding/non-breeding season according to the sex of the fish. The 'mgcv' package version 1.7 (Wood 2011) in R was used for this analysis. The 2-hourly space use estimates were transformed using a log-10 transformation to meet the assumptions of normality and homogeneity of variance. SST was dropped from further analysis because of high concurvity between SST and breeding/non-breeding season. Smoother terms were fitted to hour of the day, day length, wave height and moon illumination. The unique fish identity number was used as a random effect. The 'summary.gam' function in the 'mgcv' R packages was used to assess the significance of each of the fixed effect variables.

## RESULTS

Twenty-two eastern blue gropers *Achoerodus viridus* (35–69 cm SL) were tagged between 13 June and 27 August 2009 and passively monitored by an array of 8 receivers for 299 to 374 d (median 365 d), recording a total of 447 974 detections. Fifteen fish were caught and tagged within the no-take zone and 7 in the 'unprotected' area. Nineteen of the 22 tagged fish were detected within the reserve from the date of tagging to the final download. One fish (no. 5) was removed from further analysis because its depth records oscillated with the tides, suggesting that this fish had died. It is unknown whether it died due to effects from the tagging surgery.

### Home range size estimators and depth utilisation

From the 1000 iterations of the 2D core range analyses, 24 produced 2 candidate models with a ΔAICc of <10 and the remaining 976 iterations produced 3 models (Table 1), while all of the iterations for the 3D analyses produced 5 candidate models (Table 1). Season had the highest relative importance for the 2D core ranges (relative importance of 1.00 for all 2D models), while sex and the season × sex interaction were poor predictors (mean relative importance 0.16 [range: 0.06–0.68] and 0.01 [0.01–0.24], respectively). Sex had the highest importance for the 3D core ranges (mean = 0.82 [0.68–0.93]) followed by season (0.74 [0.55–0.95]) and the season × sex interaction (0.03 [0.02–0.05]). The 2D core ranges were significantly larger in the non-breeding season than in the breeding season, but there were no significant differences between the sexes (Table 2, all Tukey's pairwise p > 0.05). The 3D models showed that the core range was significantly smaller in the non-breeding season and males had significantly larger core ranges than females or fish of indeterminate sex in both seasons (Table 2; Tukey's pairwise p < 0.05).

Model selection for the 2D home ranges produced 3 candidate models, and 982 of the 3D iterations produced 4 models and 18 produced 5 models (Table 1). Season was the variable with the highest relative importance for both the 2D and 3D home ranges (2D mean = 1.00 [range = 1.00–1.00]; 3D mean = 0.96 [0.89–0.99]). However, sex had a higher importance for the 3D (mean: 0.95 [0.88–0.99]) than the 2D (mean: 0.71 [0.32–0.94]) home range. The season × sex interaction had a low importance for the 2D (mean: 0.27 [0.06–0.66]) and 3D (mean: 0.15

[0.08–0.27]) home range. 2D home ranges were significantly larger in the non-breeding season (Table 2), but, like the core ranges, there was no significant difference between the sexes (all Tukey's pairwise p > 0.05). Similarly, the 3D home ranges reflected the same pattern as the 3D core ranges, where the home ranges were smaller in the non-breeding season than in the breeding season (Table 2), and males had significantly larger 3D home ranges than females and fish of indeterminate sex but only in the non-breeding season (Tukey's pairwise p < 0.05). Examples of the 2D and 3D core and home ranges are given in Fig. 3a,b.

Heterogeneity between the different sexes was evident in the residuals, so a variance structure that allowed the variance to differ between the sexes was applied to the model. Model selection of 1000 iterations of the LMM produced only 1 candidate model with ΔAICc of <10, with season according to sex (i.e. an interaction between the terms) as the fixed effect (relative importance = 1.00 for all 1000 models) (Table 3). Females and fish of indeterminate sex used significantly shallower depths in the non-breeding season (Table 3; Tukey's pairwise p < 0.05), while males used deeper depths in the non-breeding season (Table 3; p < 0.001), although there was no significant difference between the sexes (Tukey's pairwise p > 0.05) independent of the breeding season.

### Home range overlap

Both 2D and 3D UDOIs produced 3 candidate models (Table 4). 2D UDOIs were significantly smaller in the non-breeding season than in the breeding season (Table 5; mean relative importance 1.00 [1.00–1.00]), and there was little support for differences between the sex pairings or the season according to the sex pairings (sex pairing: 0.01 [0.01–0.04]; season × sex pair: 0.01 [0.01–0.01]; Tukey's pairwise p > 0.05). By contrast, the 3D UDOIs showed support for a difference between sexes (mean relative importance 0.16 [range: 0.02–0.67]) and season according to sex (mean relative importance 0.17 [0.03–0.67]), although season was still the best predictor (mean relative importance 1.00 [1.00–1.00]). Like the 2D UDOIs, the 3D UDOIs showed significantly higher overlap in the breeding season than in the non-breeding season overall (Table 5), but were significantly larger for male to male pairs in the non-breeding season. Examples of the high and low 3D UDOIs and the corresponding 2D plots are given in Fig. 3c–f.

Table 1. Model candidates for linear mixed modelling analyses of 2D and 3D core and home range sizes ranked by the differences in AICc. KUD: kernel utilization density, season: breeding/non-breeding season variable, df: number of parameters in the model, n = number of model iterations (out of a total of 1000). Values are means, with ranges given in parentheses

| Model | df | AICc | ΔAICc | Model weight |
|---|---|---|---|---|
| **2D Core range (50% KUD)** | | | | |
| season (n = 999)/season + sex (n = 1) | 4/6 | 98.93 (91.51–102.76)/ 100.22 | 0.00 (0.00–0.00)/ 0.00 | 0.84 (0.43–0.94)/ 0.51 |
| season + sex (n = 999)/season (n = 1) | 6/4 | 102.53 (95.77–107.2)/ 101.17 | 0.14 (0.06–0.33)/ 0.32 | 0.14 (0.06–0.33)/ 0.32 |
| season × sex (n = 976) | 8 | 107.24 (100.61–111.79) | 0.01 (0.01–0.24) | 0.01 (0.01–0.24) |
| **2D Home range (95% KUD)** | | | | |
| season + sex (n = 730)/season (n = 184)/ season × sex (n = 86) | 6/4/8 | 99.38 (92.58–103.78)/ 100.32 (95.18–103.54)/ 99.56 (94.99–103.77) | 0.00 (0.00–0.00)/ 0.00 (0.00–0.00)/ 0.00 (0.00–0.00) | 0.48 (0.34–0.7)/ 0.44 (0.34–0.68)/ 0.44 (0.34–0.66) |
| season (n = 382)/season × sex (n = 399)/ season + sex (n = 219) | 4/8/6 | 100.55 (95.46–104.31)/ 100.06 (93.65–104.03)/ 100.63 (95.23–104.71) | 0.79 (0.01–2.5)/0.96 (0.01–2.78)/ 0.55 (0.01–2.31) | 0.31 (0.19–0.44)/ 0.3 (0.17–0.43)/ 0.34 (0.21–0.44) |
| season × sex (n = 515)/season (n = 434)/ season + sex (n = 51) | 8/4/6 | 101.54 (95.56–106.57)/ 100.87 (94.99–104.56)/ 100.84 (95.58–104.45) | 1.61 (0.06–4.48)/1.79 (0.08–4.55)/ 0.78 (0.12–2) | 0.21 (0.06–0.33)/ 0.21 (0.06–0.33)/ 0.27 (0.18–0.33) |
| **3D Core range (50% KUD)** | | | | |
| season + sex (n = 605)/sex (n = 395) | 6/5 | 504.26 (496.85–510.41)/ 506.02 (499.51–511.92) | 0.00 (0.00 – 0.00)/ 0.00 (0.00–0.00) | 0.45 (0.36–0.64)/ 0.43 (0.35–0.52) |
| sex (n = 605)/season + sex (n = 395) | 5/6 | 504.76 (498.33–511.16)/ 506.38 (499.81–512.33) | 0.50 (0.01–2.02)/ 0.36 (0.01–1.48) | 0.35 (0.22–0.42)/ 0.36 (0.24–0.43) |
| season (n = 817)/Null (n = 182)/ season × sex (n = 1) | 4/3/8 | 507.68 (500.1–514.04)/ 509.48 (503.22–514.99)/ 509.94 | 3.07 (1.61–4.76)/ 2.97 (1.89–4.03)/ 4.92 | 0.1 (0.05–0.17)/ 0.1 (0.06–0.16)/ 0.04 |
| Null (n = 792)/season (n = 183)/ season × sex (n = 25) | 3/4/8 | 508.34 (502.13–514.73)/ 509.75 (503.49–515.56)/ 507.94 (504.4–512.24) | 3.67 (1.65–5.36)/ 3.25 (1.98–4.93)/ 5.29 (4.67–5.83) | 0.07 (0.03–0.15)/ 0.09 (0.04–0.14)/ 0.04 (0.03–0.05) |
| season × sex (n = 974)/Null (n = 26) | 8/3 | 510.34 (502.69–517.17)/ 508.47 (504.59–512.41) | 5.32 (4.38–6.65)/ 5.73 (4.68–6.94) | 0.03 (0.02–0.05)/ 0.03 (0.02–0.05) |
| **3D Home range (95% KUD)** | | | | |
| season + sex (n = 1000) | 6 | 570.25 (564.47–578.56) | 0.00 (0.00–0.00) | 0.77 (0.66–0.85) |
| season × sex (n = 999)/season (n = 1) | 8/4 | 573.53 (568.41–582.09)/ 577.73 | 3.28 (1.78–4.72)/ 3.83 | 0.15 (0.08–0.27)/ 0.11 |
| season (n = 687)/sex (n = 312)/ season × sex (n = 1) | 4/5/8 | 575.36 (571.54–579.58)/ 576.79 (572.4–582.37)/ 578.47 | 5.56 (3.74–7.39)/ 5.57 (3.81–7.51)/ 4.57 | 0.05 (0.02–0.11)/ 0.05 (0.02–0.1)/ 0.08 |
| sex (n = 688)/season (n = 312) | 5/4 | 576.24 (572.48–579.77)/ 577.35 (573.08–583.17) | 6.43 (4.11–8.53)/ 6.13 (4.61–7.84) | 0.03 (0.01–0.09)/ 0.04 (0.01–0.07) |
| Null (n = 18) | 3 | 583.3 (580.86–587.31) | 9.49 (8.18–9.99) | 0.01 (0.00–0.01) |

## Space use predictors

Both analyses showed a significant decrease in space use during the non-breeding season (Table 6). For the 2D model, there was no significant difference in the space use between the sexes or tagging location (maximum p > 0.05), but the space use changed significantly across the different hours of the day, day lengths and wave heights (Table 6). Moon illumination was the only non-significant variable for the 3D models (Table 6). The estimated degrees of freedom for the smoother terms for each variable differed between the 2D and 3D models, indicating differences in the non-linear relationship for each of the significant smoother variables to space use estimates (Figs. 4 & 5, respectively).

## DISCUSSION

Aerial, arboreal and aquatic animals live in a 3D environment, and if we are to truly understand how they make use of their surroundings, it is essential that we adopt the appropriate data analysis tools

Table 2. Model averaged coefficient (β) estimates from the 2D and 3D core and home range estimates. Estimates are the square root transformed coefficients. Model parameters in *italics* indicate significant variables across all of the 1000 iterations of the model (i.e. the minimum value of the lower 95% confidence interval and the maximum upper value did not cross 0). KUD: kernel utilization density

| Model parameter | β Mean | β Range | Unconditional SE Mean | Unconditional SE Range | Lower 95% CI Mean | Lower 95% CI Range | Upper 95% CI Mean | Upper 95% CI Range |
|---|---|---|---|---|---|---|---|---|
| **2D Core ranges (50% KUD)** | | | | | | | | |
| Intercept | 3.19 | 2.96–3.34 | 0.21 | 0.18–0.30 | 2.79 | 2.37–2.98 | 3.59 | 3.49–3.72 |
| Indeterminate sex | 0.12 | -0.2 to 0.85 | 0.34 | 0.31–0.38 | -0.56 | -0.87 to 0.23 | 0.79 | 0.44–1.48 |
| Males | 0.37 | 0.04–0.49 | 0.31 | 0.27–0.34 | -0.24 | -0.6 to -0.09 | 0.97 | 0.68–1.11 |
| *Non-breeding* | 2.57 | 2.36–2.68 | 0.24 | 0.20–0.27 | 2.10 | 1.91–2.23 | 3.04 | 2.77–3.19 |
| Indeterminate sex × non-breeding | -0.25 | -1.46 to 0.55 | 0.61 | 0.52–0.70 | -1.44 | -2.63 to -0.58 | 0.95 | -0.3 to 1.76 |
| Males × non-breeding | -0.51 | -0.72 to 0.23 | 0.54 | 0.46–0.62 | -1.58 | -1.84 to -0.93 | 0.55 | 0.27–1.43 |
| **2D home ranges (95% KUD)** | | | | | | | | |
| Intercept | 2.92 | 2.66–3.16 | 0.31 | 0.24–0.34 | 2.31 | 2.10–2.69 | 3.54 | 3.21–3.66 |
| Indeterminate sex | 0.71 | 0.48–0.98 | 0.32 | 0.29–0.34 | 0.08 | -0.17 to 0.4 | 1.33 | 1.11–1.56 |
| Males | 0.66 | 0.46–0.85 | 0.28 | 0.26–0.30 | 0.11 | -0.09 to 0.31 | 1.22 | 1.01–1.41 |
| *Non-breeding* | 2.53 | 2.45–2.59 | 0.25 | 0.22–0.27 | 2.04 | 1.98–2.11 | 3.01 | 2.91–3.09 |
| *Indeterminate sex × non-breeding* | -1.27 | -1.77 to -0.86 | 0.59 | 0.51–0.64 | -2.42 | -2.96 to -1.98 | -0.12 | -0.59 to 0.37 |
| Males × non-breeding | -0.99 | -1.38 to -0.56 | 0.52 | 0.46–0.57 | -2.02 | -2.38 to -1.57 | 0.03 | -0.37 to 0.47 |
| **3D Core ranges (50% KUD)** | | | | | | | | |
| Intercept | 296.33 | 277.35–317.06 | 75.27 | 68.46–83.53 | 148.8 | 130.26–166.5 | 443.86 | 412.94–471.76 |
| Indeterminate sex | 7.56 | -16.6 to 36.32 | 94.73 | 85.94–105.45 | -178.10 | -206.12 to -147.99 | 193.22 | 165.89–234.49 |
| *Males* | 240.29 | 219.06–259.04 | 84.49 | 76.64–94.05 | 74.71 | 47.24–101.60 | 405.88 | 378.22–431.60 |
| *Non-breeding* | -62.04 | -80.49 to -38.74 | 34.61 | 29.33–41.31 | -129.87 | -153.95 to -102.90 | -18.60 | -26.43 to -13.16 |
| Indeterminate sex × non-breeding | -80.39 | -126.72 to -37.81 | 88.78 | 76.1–104.99 | -254.39 | -319.60 to -188.21 | 93.62 | 57.53–134.13 |
| Males × non-breeding | -2.70 | -50.72 to 34.98 | 79.18 | 67.88–93.64 | -157.90 | -215.83 to -110.20 | 152.49 | 99.75–204.06 |
| **3D home ranges (95% KUD)** | | | | | | | | |
| Intercept | 1026.57 | 977.08–1072.98 | 159.44 | 140.63–179.17 | 714.08 | 673.74–746.42 | 1339.06 | 1275.59–1409.39 |
| Indeterminate sex | -39.82 | -92.01 to 12.83 | 209.94 | 188.51–230.28 | -451.30 | -520.81 to -379.17 | 371.66 | 322.63–425.39 |
| *Males* | 610.97 | 552.24–662.61 | 187.25 | 168.13–205.38 | 243.98 | 170.46–311.65 | 977.97 | 929.62–1025.18 |
| *Non-breeding* | -293.54 | -330.48 to -254.53 | 86.66 | 78.09–99.25 | -463.39 | -509.07 to -423.89 | -123.69 | -163.55 to -82.17 |
| Indeterminate sex × non-breeding | -94.14 | -202.25 to 10.14 | 211.53 | 188.54–243.84 | -508.73 | -670.27 to -380.57 | 320.45 | 232.11–415.29 |
| Males × non-breeding | 237.22 | 134.05–337.57 | 188.66 | 168.16–217.48 | -132.55 | -258.61 to -12.81 | 606.98 | 511.44–707.90 |
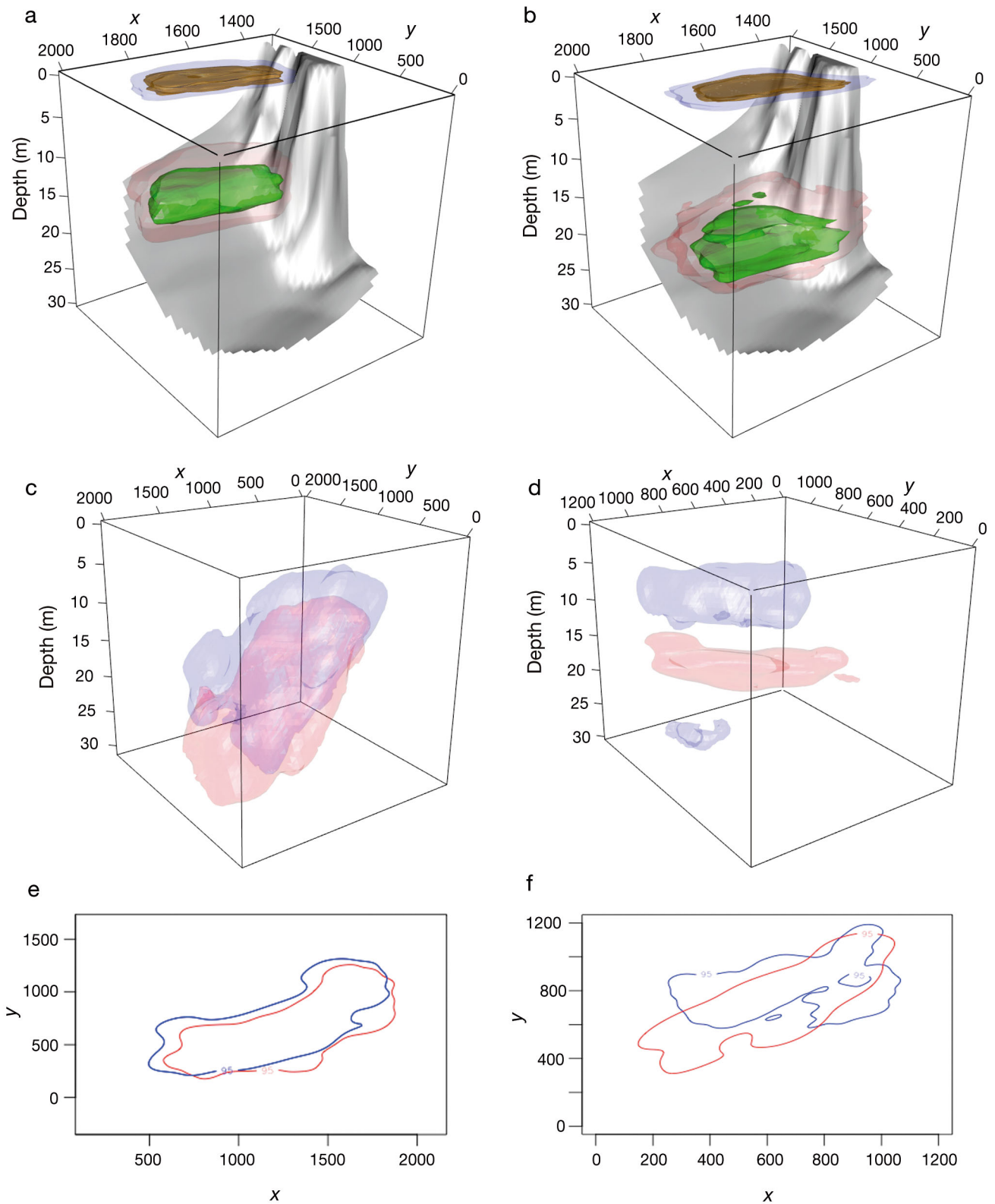
Fig. 3. Sample of (a,b) core (50% KUD) and home (95% KUD) ranges: 2D (brown and blue, respectively) and 3D (green and red, respectively) for 2 fish with the bathymetry of the reef shown in grey; (c) high 3D UDOI and (e) the corresponding 2D plot; (d) low 3D UDOI and (f) the corresponding 2D plot

Table 3. Model averaged coefficient (β) estimates from depth linear mixed models. Estimates are the square root transformed coefficients. Model parameters in *italics* indicate significant variables across all of the 1000 iterations of the model (i.e. the minimum value of the lower 95 % confidence interval and the maximum upper value did not cross 0)

| Model parameter | β | | Unconditional SE | | Lower 95 % CI | | Upper 95 % CI | |
|---|---|---|---|---|---|---|---|---|
| | Mean | Range | Mean | Range | Mean | Range | Mean | Range |
| Intercept | 3.65 | 3.65–3.65 | 0.15 | 0.15–0.15 | 3.36 | 3.35–3.36 | 3.94 | 3.94–3.95 |
| Indeterminate sex | −0.16 | −0.17 to −0.15 | 0.27 | 0.27–0.27 | −0.69 | −0.7 to −0.68 | 0.36 | 0.35–0.37 |
| Males | 0.29 | 0.29–0.30 | 0.24 | 0.24–0.24 | −0.17 | −0.18 to −0.17 | 0.76 | 0.76–0.77 |
| *Non-breeding* | −0.11 | −0.12 to −0.10 | 0.00 | 0.00–0.00 | −0.12 | −0.12 to −0.11 | −0.10 | −0.11 to −0.1 |
| *Indeterminate sex × non-breeding* | −0.05 | −0.07 to −0.04 | 0.01 | 0.01–0.01 | −0.07 | −0.08 to −0.06 | −0.04 | −0.05 to −0.02 |
| *Males × non-breeding* | 0.04 | 0.03–0.06 | 0.01 | 0.01–0.01 | 0.03 | 0.02–0.04 | 0.06 | 0.05–0.07 |

(Davis et al. 1999, Harcourt et al. 2000, Bestley et al. 2015). The present study demonstrated the importance of quantifying home range size and space use estimators using all available spatial parameters. For each of the analyses, the biological signals detected by the 2D and 3D data differed, and for the core and home ranges, the direction of the effect was in fact opposite for the 2D and 3D analyses. Given that they are likely to reflect actual use more accurately, 3D KUDs provided a superior description of spatial use by eastern blue gropers, and 3D analyses detected changes in space use that were undetected by the 2D KUDs.

2D analyses failed to detect any differences in the size of core or home ranges between sexes, yet these were readily apparent with 3D analyses. These findings were supported by the depth utilisation analyses indicating little difference in horizontal space use between sexes for these blue gropers, but that depth distribution varies between sexes. Depth is a critical dimension in a complex reef habitat, and so by incorporating depth into home range analyses, a more accurate understanding of the space requirements of

individuals can be obtained. Males had significantly larger 3D core and home ranges than females and fish of indeterminate sex. This is consistent with other studies that have evaluated intra-specific home ranges of other labrids (Jones 2005) where home range size increased with the size of the fish. Size-dependent core ranges may be due to high energetic requirements of larger fish that therefore require larger foraging areas. Gillanders (1995b) found that the feeding rate of the eastern blue groper did not change between seasons but differed significantly within each season. However, in our study, the size of core ranges changed between the breeding and the non-breeding season, suggesting that the size of foraging areas changed between seasons. This could be due to a seasonal change in diet (Gillanders 1995b), changes in movement due to spawning behaviour (Lee et al. 2015) or differing water temperatures.

Simpfendorfer et al. (2012) found that the proportion of overlap of space use differed between 2D and 3D analyses in European eels. In their study, they found that 2D space use could overestimate overlap by up to 20 % compared to 3D analyses. However, that method

Table 4. Model candidates for linear mixed modelling analyses of 2D and 3D home range overlap (utilization distribution overlap indices, UDOIs) ranked by the differences in AICc. Season: breeding/non-breeding season variable, df: number of parameters in the model. 'Sex pair' refers to the sexes of the 2 fish for which the UDOI was calculated

| Model | df | AICc | ΔAICc | Model weight |
|---|---|---|---|---|
| **2D UDOI** | | | | |
| season (n = 1000) | 4 | −16.81 (−28.38 to −6.76) | 0.00 (0.00–0.00) | 0.99 (0.96–0.99) |
| season + sex pair (n = 1000) | 9 | −8.26 (−19.28 to 1.63) | 8.55 (7.10–9.49) | 0.01 (0.01–0.03) |
| season × sex pair (n = 7) | 14 | −3.26 (−6.31 to −0.04) | 9.67 (8.94–9.99) | 0.01 (0.01–0.01) |
| **3D UDOI** | | | | |
| season (n = 996)/ season × sex pair (n = 4) | 4/14 | 45.55 (35.33–54.48)/ 46.78 (42.29–48.89) | 0.00 (0.00–0.00)/ 0.00 (0.00–0.00) | 0.83 (0.53–0.97)/ 0.57 (0.51–0.67) |
| season × sex pair (n = 996)/ season (n = 4) | 14/4 | 49.12 (41.47–41.47)/ 47.39 (42.41–49.37) | 3.57 (0.27–0.27)/ 0.61 (0.12–1.41) | 0.16 (0.02–0.02)/ 0.42 (0.33–0.48) |
| season + sex pair (n = 1000) | 9 | 53.93 (44.00–62.88) | 8.38 (7.77–9.66) | 0.01 (0.01–0.02) |

Table 5. Model averaged coefficient (β) estimates from the 2D and 3D utilization distribution overlap index (UDOI) linear mixed models. Estimates are the square root transformed coefficients. Model parameters in *italics* indicate significant variables across all of the 1000 iterations of the model (i.e. the minimum value of the lower 95% confidence interval and the maximum upper value did not cross 0)

| Model parameter | β Mean | β Range | Unconditional SE Mean | Unconditional SE Range | Lower 95% CI Mean | Lower 95% CI Range | Upper 95% CI Mean | Upper 95% CI Range |
|---|---|---|---|---|---|---|---|---|
| **2D UDOI** | | | | | | | | |
| Intercept | 0.94 | 0.93–0.96 | 0.03 | 0.03–0.04 | 0.88 | 0.87–0.89 | 1.01 | 1.00–1.02 |
| Female - indeterminate sex | 0.01 | −0.02 to 0.03 | 0.13 | 0.13–0.14 | −0.25 | −0.27 to −0.23 | 0.27 | 0.24–0.30 |
| Indeterminate sex - indeterminate sex | 0.02 | −0.02 to 0.07 | 0.15 | 0.14–0.15 | −0.26 | −0.29 to −0.22 | 0.31 | 0.26–0.37 |
| Male - indeterminate sex | 0.05 | 0.01–0.09 | 0.13 | 0.12–0.13 | −0.20 | −0.23 to −0.17 | 0.30 | 0.25–0.35 |
| Male - female | −0.02 | −0.05 to 0.00 | 0.13 | 0.13–0.14 | −0.28 | −0.31 to −0.26 | 0.23 | 0.21–0.26 |
| Male - male | 0.10 | 0.06–0.14 | 0.13 | 0.13–0.14 | −0.16 | −0.2 to 0.13 | 0.36 | 0.31–0.40 |
| *Non-breeding* | −0.21 | −0.23 to −0.18 | 0.03 | 0.03–0.03 | −0.26 | −0.29 to −0.24 | −0.15 | −0.17 to −0.13 |
| Female - indeterminate sex × non-breeding | 0.10 | 0.06–0.15 | 0.14 | 0.13–0.15 | −0.17 | −0.23 to −0.12 | 0.38 | 0.34–0.43 |
| Indeterminate sex - indeterminate sex × non-breeding | 0.16 | 0.07–0.24 | 0.16 | 0.14–0.17 | −0.15 | −0.24 to −0.05 | 0.46 | 0.39–0.54 |
| Male - indeterminate sex × non-breeding | 0.18 | 0.12–0.26 | 0.14 | 0.13–0.15 | −0.09 | −0.16 to −0.01 | 0.44 | 0.38–0.52 |
| Male - female × non-breeding | 0.12 | 0.07–0.18 | 0.14 | 0.13–0.15 | −0.15 | −0.21 to −0.08 | 0.40 | 0.35–0.45 |
| Male - male × non-breeding | 0.28 | 0.21–0.35 | 0.14 | 0.13–0.15 | 0.01 | −0.08 to 0.08 | 0.56 | 0.49–0.62 |
| **3D UDOI** | | | | | | | | |
| Intercept | 0.85 | 0.84–0.86 | 0.04 | 0.04–0.04 | 0.77 | 0.76–0.78 | 0.94 | 0.92–0.95 |
| Female - indeterminate sex | −0.05 | −0.07 to −0.02 | 0.17 | 0.16–0.17 | −0.38 | −0.4 to −0.35 | 0.28 | 0.25–0.30 |
| Indeterminate sex - indeterminate sex | −0.17 | −0.2 to −0.14 | 0.18 | 0.18–0.19 | −0.53 | −0.56 to −0.5 | 0.19 | 0.16–0.22 |
| Male - indeterminate sex | −0.05 | −0.08 to −0.03 | 0.16 | 0.16–0.17 | −0.37 | −0.4 to −0.34 | 0.26 | 0.23–0.29 |
| Male - female | −0.11 | −0.13 to −0.09 | 0.17 | 0.16–0.17 | −0.43 | −0.46 to −0.41 | 0.22 | 0.20–0.24 |
| Male - male | 0.02 | −0.01 to 0.05 | 0.17 | 0.16–0.17 | −0.31 | −0.34 to −0.28 | 0.35 | 0.32–0.38 |
| *Non-breeding* | −0.23 | −0.26 to −0.21 | 0.04 | 0.03–0.04 | −0.30 | −0.33 to −0.28 | −0.16 | −0.19 to −0.14 |
| Female - indeterminate sex × non-breeding | 0.16 | 0.11–0.21 | 0.17 | 0.16–0.17 | −0.16 | −0.21 to −0.12 | 0.49 | 0.42–0.55 |
| Indeterminate sex - indeterminate sex × non-breeding | 0.36 | 0.29–0.43 | 0.18 | 0.17–0.19 | 0.00 | −0.07 to 0.07 | 0.72 | 0.64–0.79 |
| Male - indeterminate sex × non-breeding | 0.36 | 0.29–0.43 | 0.16 | 0.15–0.17 | 0.05 | −0.01 to 0.10 | 0.67 | 0.59–0.75 |
| Male - female × non-breeding | 0.12 | 0.07–0.16 | 0.17 | 0.16–0.17 | −0.20 | −0.25 to −0.16 | 0.44 | 0.38–0.50 |
| *Male - male × non-breeding* | 0.46 | 0.40–0.51 | 0.17 | 0.16–0.17 | 0.13 | 0.08–0.19 | 0.78 | 0.71–0.84 |

Table 6. Model averaged coefficient (β) estimates and estimated df from the 2D and 3D space use additive mixed models. The model parameters in *italics* indicate significant variables across all of the 1000 iterations of the model (i.e. the maximum p < 0.05)

| Model parameter | β/estimated df | | SE | | p | |
|---|---|---|---|---|---|---|
| | Mean | Range | Mean | Range | Mean | Range |
| **2D** | | | | | | |
| Parametric | | | | | | |
| Intercept | 5.18 | 5.16–5.19 | 0.07 | 0.06–0.07 | <0.001 | <0.001 to <0.001 |
| Indeterminate sex | −0.17 | −0.19 to −0.13 | 0.09 | 0.08–0.1 | 0.07 | 0.03–0.14 |
| Male | 0.08 | 0.06–0.11 | 0.07 | 0.07–0.08 | 0.25 | 0.14–0.38 |
| *Non-breeding* | −0.13 | −0.15 to −0.11 | 0.01 | 0.01–0.01 | <0.001 | <0.001 to <0.001 |
| Non-fishing | −0.15 | −0.16 to −0.13 | 0.07 | 0.06–0.07 | 0.03 | 0.02–0.06 |
| Indeterminate sex × non-breeding | −0.03 | −0.06 to 0.01 | 0.02 | 0.02–0.02 | 0.19 | 0.00–0.96 |
| Male × non-breeding | 0.05 | 0.02–0.08 | 0.02 | 0.02–0.02 | 0.02 | 0.00–0.33 |
| Smoother | | | | | | |
| *Hour* | 8.35 | 7.97–8.64 | | | <0.001 | <0.001 to <0.001 |
| *Length of day* | 7.32 | 4.35–8.43 | | | <0.001 | <0.001 to <0.001 |
| Moon illumination | 1.87 | 1.00–4.42 | | | 0.12 | 0.00–1.00 |
| *Wave height* | 1.21 | 1.00–5.34 | | | <0.001 | <0.001 to <0.001 |
| **3D** | | | | | | |
| Parametric | | | | | | |
| Intercept | 3.21 | 3.19–3.22 | 0.23 | 0.23–0.24 | <0.001 | <0.001 to <0.001 |
| *Indeterminate sex* | −0.89 | −0.91 to −0.87 | 0.31 | 0.31–0.32 | <0.001 | <0.001 to 0.01 |
| *Male* | 0.59 | 0.57–0.62 | 0.25 | 0.24–0.25 | 0.02 | 0.01–0.02 |
| *Non-breeding* | −0.48 | −0.50 to −0.46 | 0.04 | 0.04–0.04 | <0.001 | <0.001 to <0.001 |
| Non-fishing | 0.52 | 0.5–0.54 | 0.23 | 0.23–0.24 | 0.03 | 0.02–0.03 |
| *Indeterminate sex × non-breeding* | −0.20 | −0.23 to −0.18 | 0.05 | 0.05–0.05 | <0.001 | <0.001 to <0.001 |
| *Male × non-breeding* | 0.55 | 0.52–0.57 | 0.06 | 0.06–0.06 | <0.001 | <0.001 to <0.001 |
| Smoother | | | | | | |
| *Hour* | 8.76 | 8.74–8.78 | | | <0.001 | <0.001 to <0.001 |
| *Length of day* | 5.98 | 4.05–7.52 | | | <0.001 | <0.001 to <0.001 |
| Moon illumination | 1.02 | 1.00–1.59 | | | 0.4 | 0.22–0.73 |
| *Wave height* | 3.01 | 2.68–3.32 | | | <0.001 | <0.001 to <0.001 |

does not take into consideration the individuals' utilization distribution and may overestimate the degree of overlap (Fieberg & Kochanny 2005). In order to avoid overestimation of the degree of overlap, Fieberg & Kochanny (2005) suggested using overlap indices that are a function of an animal's utilization distribution, such as the UDOIs used in the present study. With UDOIs, we found larger variation in the 3D compared to the 2D UDOIs (Fig. 3c–f). However, similar to the core and home range estimates, we found that 2D UDOIs were only able to detect a seasonal difference in the degree of home range overlap, whereas the 3D UDOIs also showed a difference between sex pairings according to season (male to male UDOI was significantly higher in the non-breeding season). Therefore, both home range and UDOI results show the importance of using 3D analyses to detect fine-scale changes in movement parameters.

Territoriality and dominance hierarchies are frequently observed in protogynous fish species (Pastor et al. 2009, Raposeiro & Azevedo 2009, Kline et al.

2011). Terminal phase males will usually aggressively defend a territory against intruders and the largest female (see Kline et al. 2011 and references within). If eastern blue gropers had displayed strong, territorial behaviour, we would have expected males to have very little home range overlap with other males but higher overlap with females. However, males showed higher degrees of overlap with other males compared to females and fish of indeterminate sex. In addition, the only seasonal change between the sex pairings was evident between males. This suggests that males do not have a fixed territory and their movements do overlap with other males. We suggest that they may defend these areas less aggressively than observed in other protogynous fish species outside of the breeding season. However, the 3D home range size of males decreased during the breeding season, which may indicate that the males form nests and remain in their vicinity throughout the breeding season, similar to the behaviour observed in axillary wrasse *Symphodus mediterraneus*
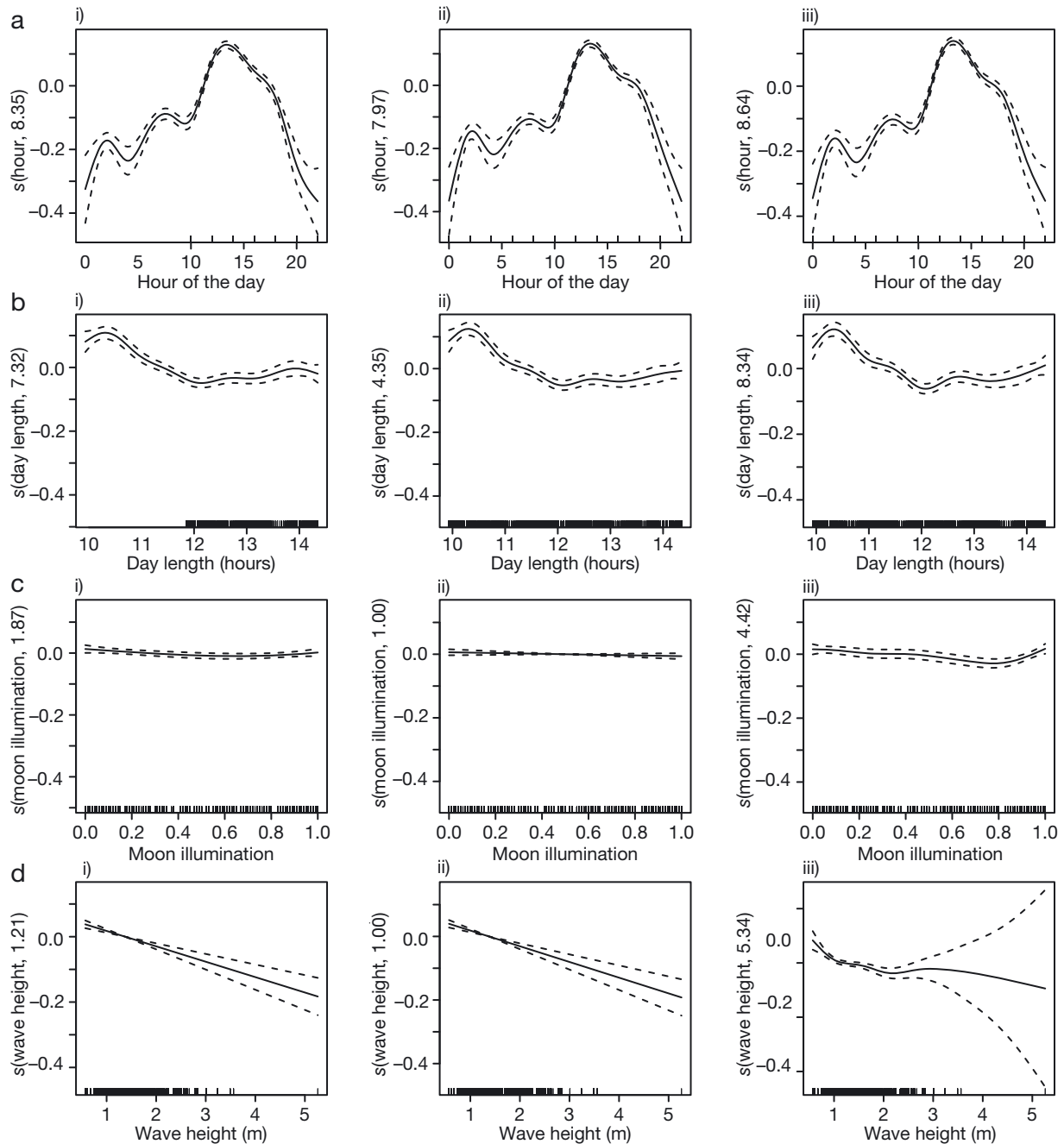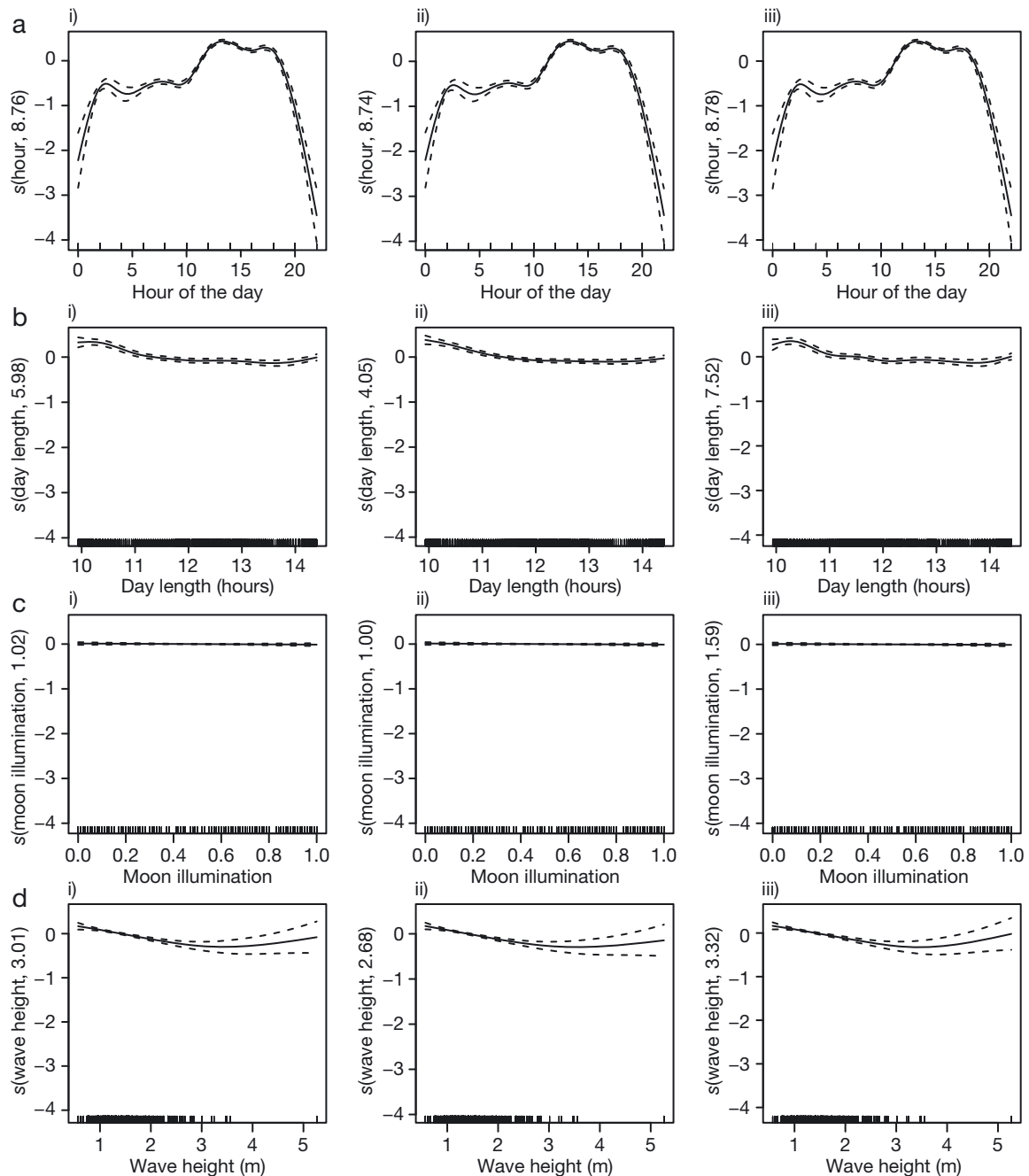
Fig. 4. Plots of the smoother (*s*) terms in the generalised additive mixed modelling for 2D space use estimates for the model with the (i) mean, (ii) minimum and (iii) maximum estimated degrees of freedom for (a) hour of the day, (b) day length, (c) moon illumination and (d) wave height. Plots are interpreted relative to 0 with values >0 indicating statistical significance

(Raposeiro & Azevedo 2009). Alternatively, this decrease in home range size, along with the decrease in 3D UDOIs in the breeding season, could indicate that male eastern blue groper only form and defend territories during the breeding season. This is opposite to findings in other Labridae, which suggested that territoriality amongst smaller species is not linked to

reproduction but to foraging or habitat preferences (Mumby & Wabnitz 2002). Females and indeterminates had larger home ranges and higher overlap with all other fish during the breeding season, suggesting that these individuals increase their space use to spawn with multiple individuals, similar to California sheephead *Semicossyphus pulcher*

Fig. 5. Plots of the smoother (*s*) terms in the generalised additive mixed modelling for 3D space use estimates for the model with the (i) mean, (ii) minimum and (iii) maximum estimated degrees of freedom for (a) hour of the day, (b) day length, (c) moon illumination and (d) wave height. These are interpreted relative to 0 with values >0 indicating statistical significance

(Adreani et al. 2004). While UDOIs were used to assess territoriality of a reef fish in this study, this metric can also be used for a variety of purposes, such as to examine predator–prey distributions (Thomas et al. 2011), fisheries interactions (Delord et al. 2010) or niche partitioning between competitors (Thiebot et al. 2011). These techniques can also be readily extended to other space use metrics, such as Bhattacharyya's affinity, to assess the similarity of utilisation distributions (Fieberg & Kochanny 2005). We suggest that where the data are available and suitable for the study species, 3D data should be used for such analyses to ensure a true representation of the animal's movement.

3D estimates showed a clear increase in space use during daylight hours, which was not detected using the 2D analysis. Night-time refuging appears common in many labrids (Bryars et al. 2012), and would cause the acoustic signal to be blocked by the sheltered areas. Although this pattern was detected by both the 2D and 3D analyses, the results from the 2D analysis suggest that eastern blue gropers increase their space use later during the day. Although Gillanders (1995a) found that eastern blue groper did not change feeding rates throughout the day, further observational studies would need to be conducted to assess whether the 2D or 3D estimates were more realistic representations of the behaviour. However, 3D space use was significantly different for the fish tagged in the no-take area and the 'unprotected' area, and again the 2D analysis failed to detect this. In sum, this study comprehensively demonstrates that ignoring an entire dimension (in this case depth) when investigating space use in a 3D world may reduce statistical inference and therefore overall understanding of animal behaviour.

The few previous studies that have used 3D space use modelling of aquatic species have done so on species that use different depths within the water column (e.g. Harcourt et al. 2000, Simpfendorfer et al. 2012, Bestley et al. 2015). However, our study of blue groper shows that such analyses are just as important for understanding the movement of a demersal reef-dwelling species, as these fish evidently use the high relief of the reef in a similar manner. At the same time, the heterogeneity of a reef environment may present limitations for studies using technology such as passive acoustic telemetry, as the reef may cause areas of 'acoustic shadowing', and a tagged animal may not be detected where complex reef outcrops are present. We deployed receivers away from reef outcrops and above the seabed in order to minimise this effect, as the detection range of receivers decreases when deployed close to the sea floor (Huveneers et al. 2016). Environmental conditions can also affect the ability of receivers to detect tagged organisms and need to be accounted for in acoustic telemetry studies (Gjelland & Hedger 2013, Simpfendorfer et al. 2015, Huveneers et al. 2016). Sentinel tags were deployed and receiver detection range tested to account for these limitations and demonstrated that in this array tagged eastern blue groper were still detected within 300 m in the worst weather conditions. However, during periods of good weather, the detection range of the receivers may extend beyond the 300 m range (Farmer et al. 2013) and thus would introduce further variability in the horizontal positioning in the 2D and 3D estimates.

Many designs in acoustic telemetry studies do not allow precise positions of tagged organisms to be estimated. Here, we proposed a new method using a randomisation process to calculate position of eastern blue groper and address this limitation. Fine-scale positioning systems (e.g. VR2W Positioning System, Espinoza et al. 2011; or older Vemco Radio Acoustic Positioning system, Huveneers et al. 2013) could be used to further refine the precision of position estimates, but these approaches require more acoustic receivers or a different system.

The present study shows that analysing the space use of animals in relation to their 3D environment provides a better understanding of environmental drivers influencing their movement. It has been suggested that space use studies should focus less on the absolute extent of an animal's movement, with more emphasis on important biological signals within the data (Signer et al. 2015). We have demonstrated how important it is to incorporate all spatial dimensions to detect changes in space use even in a demersal fish species. This may be important for effective decision making when managing wild populations and may aid in predicting habitat use and species occurrence (e.g. Avgar et al. 2013), use of foraging 'hotspots' (e.g. Block et al. 2011, Bestley et al. 2013, 2015) or identification of ecological 'hotspots' (Block et al. 2011). Identifying such areas may be masked if the full spatial extent of an animal's movement is not considered, as we saw with our 2D analyses. Such assessments will become increasingly important for effective monitoring of how species and populations adapt under changing environmental conditions induced by climate change.

## CONCLUSION

Biotelemetry has become an increasingly popular and powerful tool for many biological research questions, over a wide range of taxa (Hussey et al. 2015). However, a common limitation of biotelemetry studies is the high cost associated with such data collection, often leading to low sample sizes and reduced power of statistical inference (Cooke et al. 2004, Hebblewhite & Haydon 2010). This, coupled with the ethical and welfare issues associated with tagging animals, especially endangered or vulnerable species/populations (Cooke 2008), accentuates the importance of being able to infer as much, and as accurately, as possible from the data obtained. In this study, we have unequivocally shown that commonly used 2D analyses were unable to detect statistical

differences clearly apparent with 3D analyses, demonstrating the importance of using 3D analyses to determine space use parameters for species inhabiting 3D environments. While these techniques were applied to a marine species, the analyses used in this study are equally applicable to other species in other environments where a third spatial dimension might be of importance, such as aerial and arboreal animals.

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